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Trace mineral metabolism in different livestock species: more common or more divers?

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Uniformity of basal components of trace mineral metabolism

Trace minerals are part of living systems since the very early steps of the evolution of biological life. An example of archaic trace minerals is zinc (Zn). One of its fundamental functions is control of gene activity and gene repair systems through Zn finger proteins (Emerson and Thomas, 2009). Interestingly, Zn finger motifs in all known types of living organisms (eukaryotes and prokaryotes) in the earth's biosphere (Nagel et al., 2019). This suggests that Zn finger proteins already established in the joint ancestor of all contemporary forms of living beings on our planet. Zn finger proteins are an example of deep uniformity of metabolic trace mineral principles.

Iron (Fe) is another example of uniformity of metabolic trace mineral principles. The hem motif with Fe as its central atom is common to all aerobic organisms including plants and may be found e.g., in the cytochromes of the mitochondria, and the catalases (Harel et al., 2014). In addition, copper (Cu) and manganese (Mn) exert uniform biological functions in aerobic organisms when handling oxygen, e.g., in antioxidative defense systems, when assisting Fe metabolism through control of its oxidative status (Aguirre and Culotta, 2012; Ruiz et al., 2021). Oxygen transport systems, however, present an interesting diversity among groups of animals. While mollusks and insects including spiders employ Cu (hemocyanine), and other marine invertebrates like worms use Fe in non-heme proteins (hemerythrin), all vertebrates make use of Fe bound within the heme-motif (hemoglobin) (Loehr, 1988). Obviously, oxygen transport systems are evolutionary spin offs from basic heme proteins (cytochromes, catalases, etc.). Within vertebrates, however, function and structure of oxygen transport proteins is uniform.

Another type of uniformity arises from the fact that all essential trace minerals exert a high toxic potential to protein structures, particularly those from the group of transition metals (National Research Council, 2005). Through formation of unintended chelates, they may impair functions of proteins and produce oxidative stress while changing the oxidative status (e.g., Fe). Therefore, metabolic handling of essential trace minerals requires tight control of influx, outflow, and concentrations in the biological compartments. This so-called homeostatic regulation principle is uniform among animals (Brugger et al., 2022).

Challenges to trace mineral metabolism of terrestrial animals

Indeed, the concentrations of essential trace minerals in seawater may vary depending on geographical and climatic factors. However, these variations are much smaller compared to the situation on land. Here, virtually distilled water (precipitation) gets into contact with a wide range of different surface materials (rocks, soils, etc.) that release trace minerals in different quantities and chemical conformations. Furthermore, contact with aerial oxygen may massively vary with time and location and may induce changes in oxidative status that differentially affect mobility of trace minerals in soils. This entails enrichments or washouts of trace minerals in/from the soils, depending on their chemical nature, the pattern of precipitation, and the mineral supply through weathering from the geogenic underground. Differentiation of soil trace minerals (concentration, mobility) may affect respective concentrations in plant materials and hence the feed chain of all animals. These mechanisms are most obvious for Fe, Iodine (I), and Selenium (Se). While Fe is usually highly enriched, I and often Se is much less present on dry land compared to seawater (Jurinak and Tanji, 1992).

The surface of plant materials is inevitably covered with a layer of dust from soils that may contain Fe at high concentrations. This Fe often contributes to total Fe load of herbivores to a much higher extent than the plant material itself and silage fermentation has been shown to increase its solubility (Hansen and Spears, 2009).

Iodine from the ocean may be transported by water droplets through wind from the shore into the land for up to around 50 to 100 km. However, the land behind is regularly poor in iodine (Suess et al., 2019). Animals living on land needed to develop highly efficient systems to extract and to store the tiny amounts of iodine circulating in the plant biosphere (sodium/iodide symporter (NIS), thyroid gland). Another challenge is preferential I supply to the offspring because iodine deficiency is detrimental for their early development. Animals hatching eggs such as birds solved this challenge through high NIS expression in the ovary. Interestingly, mammals did the same in the mammary gland (Dohán et al., 2003; Concilio et al., 2020). This homologous solution of the same challenge seems to be a remarkable diversification between groups of species. However, it may be explained also as “simply” switching off the homeostatic control of I metabolism in tissues, which are most responsible for supply of iodine to the offspring, rather than the establishment of a new metabolic tool.

In case of Se, all metabolic functions depend on Se cysteine, which is formed by fixation of inorganic Se into proteins along with a complex posttranslational modification. The only way to store Se in the body is erroneous incorporation of Se amino acids into protein synthesis, a feature which is the primary mode of Se toxicity (EFSA, 2012). Under natural conditions, also Se intake occurs mainly as Se amino acids that again were erroneously incorporated into the protein of feed materials of plant or animal origin, respectively. Therefore, Se deficiency and toxicity are quite close to each other (Suttle, 2010). All these aspects give rise to the hypothesis that essentiality of Se might be rather young from the viewpoint of evolution, and that diversity between species in handling Se is comparably less pronounced.

Characteristics of trace mineral metabolism in ruminants

Bovidae are a rather young group of ruminants, which co-evolved with grasslands around 20 million years ago (Hackmann and Spain, 2010). Microbes in the forestomachs ferment around two thirds of ingested feed materials into gases (mainly CO₂), volatile fatty acids providing feed energy, and microbial matter providing protein. Dietary trace mineral chelators such as e.g., phytic acid, also undergo microbial degradation. This may in general improve the bioavailability of dietary Zn and other phytate sensitive trace minerals (Humer and Zebeli, 2015).

However, strongly reducing conditions in the forestomachs may also entail negative effects. For example, selenate and selenite are reduced to selenide, thereby passing gaseous Se⁰, which might get lost. Uptake of Se via Se-amino acids, as it is the case under natural conditions, remains unaffected since it is already reduced. Part of the ingested Se-amino acids are transferred from the feed material into microbial protein (Spears, 2003; Galbraith et al., 2016).

Cu is the most prominent victim of reductive processes in the forestomachs. It entails a drastically reduced solubility that remains virtually irreversible to the subsequent digestive processes in case of formation of sulfates and molybdates (Spears, 2003). High dietary Fe exposure (mainly via dust on surface of plant feed materials) further constrains Cu absorption (Standish et al., 1969). Therefore, ruminants face scarcity of bioavailable dietary Cu in principle. Dietary Cu excess, however, is rather unlikely under natural conditions, and at the same time ruminants are known for their pronounced sensitivity to Cu intoxication (National Research Council, 2005; Suttle, 2010). Apparently, ruminants lost the metabolic capability of Cu homeostasis to excrete excessive intakes due to lack of an evolutionary pressure.

Aspects of trace mineral metabolism of livestock animals in modern production systems

Compared to their ancestors, modern livestock animals show significantly higher performance at still similar levels of feed intake. Accordingly, the minimum concentration of dietary trace minerals ensuring an adequate supply has been steadily increasing during past decades. Nowadays, it exceeds native dietary levels in most cases and requires targeted supplementation, which is usually applied as mixtures of pure (in)organic formulations of different elements together with vitamins (Brugger et al., 2022). This practice may promote undesirable redox reactions already in the diet. Furthermore, the spectrum of feedstuffs changed drastically, especially for swine and poultry, which are today reared on base of cereals and legumes. This practice introduces significant amounts of phytic acid, which is a strong chelator particularly to Zn, thereby exacerbating the necessity for trace mineral supplementation (Boerboom et al., 2022). Another significant interaction with feed-born antinutrients are glycosinolates, e.g., from rape seed extracts used as dietary protein sources. It massively modulates the transfer rate of added dietary I into milk and eggs, respectively (Franke et al., 2009; Flachowsky et al., 2017). Regarding feed intake, the picture is somewhat different to lactating livestock (cows, sows). Particularly in dairy cows, feed intake increases dramatically with the onset of lactation compared to the preceding gravidity. This accelerates the passage rate of feed through the forestomachs and hampers the degradation of feed-born chelators such as phytate. Accordingly, trace metal requirements per kg of feed may increase, particularly for Zn. This may explain reports of reduced mastitis incidences in high yielding dairy cows receiving higher Zn supplementations (Cope et al., 2009). On the other hand, lactating cows ingest a multiple of trace mineral quantities compared to maintenance levels because trace mineral are usually supplemented on base of presumably adequate concentrations per kg of feed. Recent research addresses the question whether the enormous quantities of trace minerals consumed by high yielding dairy cows might overload their homeostatic regulation capacities and might entail e.g., inadequate tissue accumulations and oxidative stress.

Conclusions

Trace mineral metabolism exhibits diversifications between groups of species as well as between living conditions (nature vs. agriculture). They arise mainly from features of the ingested feed as well as from the special properties of the digestive tract (ruminants). After absorption, the metabolic principles seem to be rather uniform. Indeed, the capability of species to cope with trace mineral excess may vary, but this remains a quantitative variation of the same metabolic principle.